Pedobiologia 25, 235—240 (1983)

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Winter strategy of surface dwelling Collembola[1])

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With 2 figures

1. Introduction

Winter conditions are unfavourable for normal insect activity and development. In Norway, no species seems able to carry out more than minor parts of its life cycle during that season. Most insects have some kind of winter dormancy. However, it has long been known that some insects ar . .ctive on the snow during thaw LATZEL 1907, CHAPMAN 1954, STRÜBING 1958). More rec ntly it has also become apparent that a wide variety of insects are active in the subnivean space (NÄSMARK 1964, AITCHINSON 1979), and even inside the snow pack (BRUMMER-KORVENKONTIO & BRUMMER-KORVENKONTIO 1980, LEINAAS 1981a). What various species actually do in winter is in many cases fairly well described, but much less is known about why they do it.

During studies of epedaphic (surface dwelling) Collembola, I have been concerned about which aspects of the life history that may be timed to winter, and how it is optimal to spend the winter. The present paper refers mainly to studies done in a spruce forest (200 meters. a.s.l.) in Eastern Norway. The snow cover stabilizes the subnivean temperature around —1 to 0 °C during most of the winter, but may occasionally fall below —5 °C when low air temperature coincide with a thin snow cover (LEINAAS 1981a). Even the winter active collembolan species show little feeding activity and no development seems to occur. Their winter strategies, therefore, not only include how to survive and choice of specific activity patterns, but also how to prepare for developmental arrest, e.g. by going into diapause. To understand these strategies as adaptations to a seasonal environment one has to focus attention on their consequences for the insects in their next growth season.

2. Physiological adaptations to stress factors

Collembola survive cold by supercooling (SØMME & CONRADI-LARSEN 1977a). By simply emptying their guts of foreign freezing nuclei, they may obtain supercooling points of —15 to —25 °C (SØMME & BLOCK 1982). This is more than sufficient for most species that are protected by a snow cover, suggesting that winter temperature is not a very critical factor for these species. However, in habitats penetrating the snow cover, like tree trunks and boulders, the temperature may frequently fall well below the values mentioned above. Species of such habitats, therefore have either to seek protection on the ground during winter, or to increase their ability to supercool to around —35 to —40 °C. The latter solution is obtained by accumulating cryoprotective substances, usually glycerol, in late autumn (SØMME & CONRADI-LARSEN 1977a). The choice of either of these solutions seems in some way to depend on the summer ecology of the species. Species overwintering on exposed sites (e.g. *Xenylla maritima* TULLBERG, *Anurophorus laricis* NICOLET, *Vertagopus westerlundi* REUTER) carry out their entire life cycle in these habitats. By remaining there in winter, they may benefit from an early spring. In late winter the temperature may frequently exceed 10 to 20 °C on such sites while the ground is still covered by deep snow. This, how-

[1]) Contribution to the Vth International Colloquium on Apterygota, Louvain-La-Neuve, Belgium (23—26 August 1982) organized by C. GRÉGOIRE-WIBO and PH. LEBRUN.

ever, will vary greatly from year to year. On the other hand, species that seek protection on the ground reproduce in the soil during spring, although they temporarily return to their exposed habitats in late winter. This includes *Hypogastrura inermis* (TULLBERG), *Isotoma violacea* TULLBERG, *Entomobrya nivalis* L., *E. marginata* (TULLBERG). I suggest that since their phenology is dependent on when the ground becomes free of snow, they have a limited possibility to benefit from exceptionally early warm periods above the snow. This may explain why evolution has not favoured the costly increase in cold hardiness that would have been necessary in order to overwinter on their main habitat.

Locally, oxygen deficits may occur, especially where animals are trapped under compact ice. Species hibernating in such places are able to survive anaerobic conditions for long periods (SØMME & CONRADI-LARSEN 1977b, LEINAAS & SØMME 1983).

3. Activity vs. inactivity

None of the winter active Collembola seem to be strictly associated with the subnivean space. Nearly all the epedaphic species I have studied (LEINAAS 1981a) move up to the lowest part of the snow profile, and few or no individuals are found on the soil surface. I have explained the migration into the snow as an adaptation to avoid conditions like alternating water-logging and freezing of the soil, with formation of compact ice on the top (LEINAAS 1981a). These conditions depend on extensive periods of thaw followed by cold. They are unpredictable, but most likely to occur in late winter. Presumably because of this unpredictability, the escape reaction is initiated in early winter. Good drainage in the snow prevents formation of compact ice and water-logging there. By their behaviour, therefore, the animals are bound to be above the critical zone whenever these conditions occur. The very few species that remain on the ground appear to stay inactively in the litter (e.g. *Anurophorus septentrionalis* PALISSA, *Hypogastrura inermis*, *Xenylla boerneri* AXELSON). This seems energetically favourable for species remaining on the ground, since little or no feeding occur, during winter in the present study area (LEINAAS 1981a). Inactivity also gives the best protection from predators (ERNSTING *et al.* 1977). These species have to be physiologically adapted to subnivean conditions, but this requirement seems reduced by the fact that they usually hibernate in well drained sites like needle litter at the base of trees.

Arguments concerning subnivean conditions do not explain why some species emerge on the snow surface during thaw. In contrast to most other snow active insects (see STRÜBING 1958), Collembola do not seek mating partners during winter. In *Hypogastrura socialis* (UZEL) and *H. lapponica* (AXELSON), the winter activity is clearly dispersal behaviour (LEINAAS 1981a, b). During summer they form aggregates coordinated by pheromones at specific sites. In winter the coordination of activity stops and the animals become dispersed on the snow surface. In spring they once more aggregate on early snow free patches. Prior to dispersal both species attain specific winter forms and change back to the summer form in spring (i.e. cyclomorphosis). The winter forms appear morphologically adapted to activity on the snow surface (LEINAAS 1981b, c).

Presumably, the patchy habitats of these species favour a high dispersal ability (MACARTHUR & WILSON 1967), and several factors may have favoured timing of dispersal to the winter. The smooth snow surface makes migration easy in winter compared to the obstacles offered by vegetation, water etc. during summer. It also seems optimal to migrate in periods when reproduction and feeding do not occur (JOHNSON 1969), and when the insects in any case would have to leave their summer habitats owing to unfavourable winter conditions. Moreover, the risk of predation seems minimized by migrating in winter.

Most snow surface active species belong to the genus *Isotoma*. Their affinity towards the snow surface, however, varies greatly, apparently to some extent being dependent on their distribution patterns. Species of the *violacea*-group show distinct habitat preferences, usually with a patchy distribution. Next to *H. socialis*, they are the most common Collembola on the snow in Norway. Several of the species are cyclomorphotic, with a specific winter form (FJELLBERG 1976, LEINAAS 1980). In contrast, *I. viridis* BOURLET is a typical gen-

eralist which is often continuously distributed over a wide range of habitat types, and therefore has relatively little need for a specific dispersal stage. The winter activities of these species have been compared in two biotopes: In the spruce forest, *I. violacea*, *I. hiemalis* SCHOETT and *I. blekeni* LEINAAS of the *violacea*-group were commonly observed on the snow, while the coexisting *I. viridis* was never seen there. In a garden, *I. viridis* is a dominant epedaphic species in various habitat types. In contrast *I. germanica* HUETHER et WINTER of the *violacea*-group is very difficult to find in summer apparently owing to extremely patchy distribution. During winter, however, *I. germanica* is the most numerous Collembola on the snow all over the area, while *I. viridis* only occurs in small numbers on the snow surface. Another specialist, *I. olivacea* TULLBERG is associated with humid habitats. In winter, however, I have found specimens more than 50 metres away from such environments, in areas too dry in summer to be inhabited by the species then. These observations support my suggestion that activity on the snow surface is an adaptation for dispersal. However, the scant information on their general ecology gives no answer as to why *I. hiemalis* is more active on the snow surface than the much more patchily distributed *I. blekeni*, and why *I. tigrina* (NICOLET) of patchy habitats like compost heaps, is not active on the snow surface at all.

In the spruce forest studied, *Entomobrya nivalis* and *E. marginata* coexist on tree trunks and at the base of the trees during summer, and both species move down to the ground at the onset of winter (LEINAAS & BLEKEN unpubl.). Later in winter, however, they differ totally in behaviour. *E. nivalis* moves away from the trees, is active on the snow surface during thaw and moves back to the trees along the snow surface in late winter. *E. marginata* on the other hand, almost exclusively hibernates in the litter at the base of the trees, and reinvades the trees, often up through the snow, at about the same time as *E. nivalis*. Like the *Hypogastrura* and *Isotoma* species mentioned above, the winter activity of *E. nivalis* results in a dispersal. It enables the species to colonize new trees as these, during succession, become favourable summer habitats. The advantage of this behaviour seems more understandable than the lack of winter activity in *E. marginata*. Being associated with the same patchy habitat and even more strongly corticole than *E. nivalis*, one would expect *E. marginata* to have at least the same need for dispersal as the latter. Before going deeper into this problem, more knowledge is needed of their summer ecology, especially about their distribution and dispersal ability in the earlier stages of forest succession.

4. Diapause or quiescence? Strategies for developmental arrest

I have not observed any development in Collembola during winter. Two alternative main strategies for such dormancy may be distinguished — diapause and temperature quiescence.

Temperature quiescence is a simple developmental arrest during periods of low temperature. It may occur in any developmental stage and will therefore hardly affect the population phenologically. Diapause, on the other hand, is restricted to specific stages of development, in which the population gradually will become synchronized during the autumn. Unlike most insect groups, however, the autumn populations of Collembola usually consist of many age classes. Often the youngest ones are not affected by diapause, but overwinter in a state of temperature quiescence. Apparently these stages do not suffer from higher mortality than the diapausing animals. Therefore, the adaptive significance of winter diapause in Collembola has not been related to winter survival, but to its phenological consequence (LEINAAS & BLEKEN 1983). Termination of the diapause may time start of a specific life history event to spring. The life strategy of a population therefore not only concerns whether to have a diapause or not, but also at which developmental stage it should occur and the degree of synchrony to be obtained.

A fixed phenology, as obtained by winter diapause, is believed to be advantageous in fluctuating environments that will affect age classes differentially (MACARTHUR 1968). Timing of egg hatch seems to be a crucial point in this connection, ensuring that the sensitive first instars emerge under favourable conditions (LEINAAS & BLEKEN 1983).

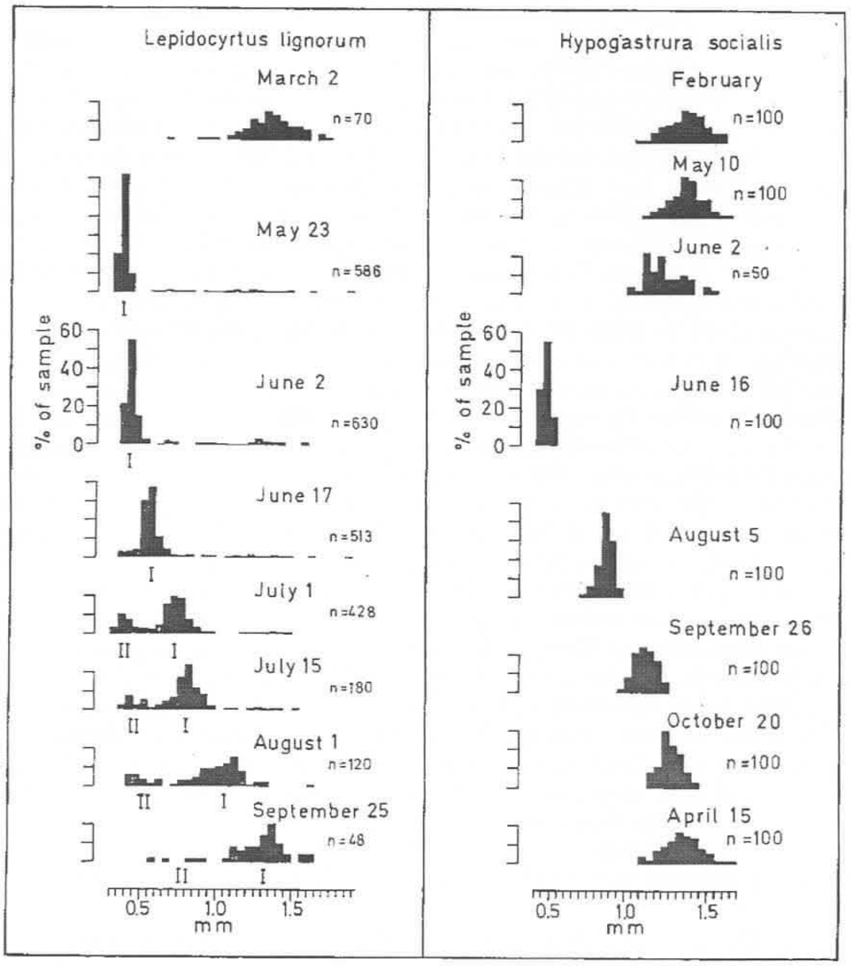

Fig. 1. Size distribution (in body length) within the populations of *Lepidocyrtus lignorum* (during 1978) and *Hypogastrura socialis* (1979—1980), from a spruce forest. n = No. of animals measured. I, II = indications of cohort I and cohort II of the 1978 generation of *L. lignorum*.

It should be noted that diapausing animals are not necessarily inactive.

Phenological events in the populations of *Lepidocyrtus lignorum* (Fabricius) and *Hypogastrura socialis* from the same forest, are illustrated by their body size distribution (Fig. 1). *L. lignorum* shows a dimorphic reproduction pattern, resulting in two distinct cohorts each year. The first one (I) emerges from overwintering eggs that are synchronized by a diapause. The second cohort (II) results from spring reproduction of animals that have been in reproductive diapause since autumn. Cohort I hatches earlier than all potentionally competing species. This phenological difference might possibly reduce interspecific competition and thus the mortality in the population (Hutchinson 1951, MacArthur 1972). In agreement with this suggestion, cohort I was found to have a markedly lower mortality than cohort II, which hatches at the same time as most other epedaphic species. Regardless of whether or not this difference in mortality is in fact caused by competition, it shows that hatching of *L. lignorum* is timed to an optimal period by egg diapause. Under certain environmental conditions, however, the survival changes in favour of cohort II. This was for instance observed after clearcutting part of the area (Leinaas & Bleken 1983). Such fluctuating selective pressure may explain the dimorphic winter strategy with both egg diapause and reproductive diapause in the population.

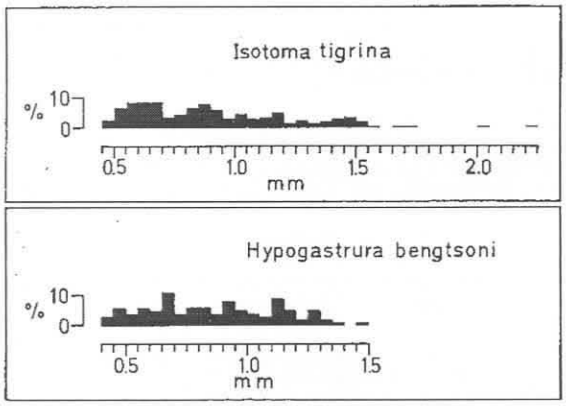

Fig. 2. Body size distributions within populations of *Isotoma tigrina* and *Hypogastrura bengtssoni*. Material collected in compost under snow April 8, 1978.

The synchronized egg hatch in *H. socialis* is caused by a uniform termination of a reproductive diapause, and the fact that all animals only reproduce once. If *H. socialis*, like most Collembola, had reproduced several times, the hatching period would have been prolonged correspondingly. The synchronization in *H. socialis* is related to its coordinated age specific behaviour patterns, which require that all individuals in a colony are of equal age (LEINAAS unpubl.). As seen in *L. lignorum*, egg diapause may synchronize the hatching of eggs that are laid during a long period in autumn. This solution, however, is not feasible in *H. socialis*, where the winter activity is a fundamental part of the life strategy. Thus, to possess both winter activity and a synchronized hatching, it is necessary to have a reproductive diapause with the cost of only one reproduction.

Some species have long reproductive periods favoured through e.g. spreading the risk of hatching during unpredictable adversed periods, reducing intraspecific competition or maintaining high reproductive potentional at any time. I have found prolonged reproduction particularly pronounced in populations of compost forms. They live in an environment of moderate seasonality and unpredictable, dramatic perturbations; this presumably favours opportunistic life strategies (PIANKA 1978). For instance, both *Isotoma tigrina* and *Hypogastrura bengtssoni* (ÅGREN) overwinter in most size classes (Fig. 2), and according to my preliminary studies, without diapause.

5. Conclusion

In Norway, Collembola do not reproduce or develop during winter, and they scarcely feed until the end of the season. No density dependent limiting factor seems important in this period. I have examined the winter strategy of the surface dwelling species by the questions; how to survive, how to be active and at what stage(s) and physiological state(s) should developmental arrest occur? The answer to these questions may be found by studying winter populations. The ultimate reason for a specific winter strategy, can, however, in most cases, be understood only by studying the animals during summer (i.e. when they feed, reproduce, are preyed upon and possibly compete). As stressed in this paper, such information is very much needed to increase our understanding of the winter ecology of the species.

6. Zusammenfassung

Winterstrategien von epigäisch lebenden Collembolen

Die Überwinterungsstrategien von epigäisch lebenden Collembolen werden als eine Reihe von Adaptationen beschrieben, die bei winteraktiven Tieren beobachtet wurden. Diese Adaptationen spielen in der Lebensgeschichte dieser Arten eine unterschiedliche Rolle: Winterhärte, Anaerobiosis und die Fähigkeit, geschützte Überwinterungsorte auf dem Boden oder im Schnee aufzusuchen,

sind für das winterliche Überleben wichtige Faktoren. Viele Arten mit nesterartiger Verbreitung in ihren Sommer-Habitats kommen im Winter weit verstreut vor. Die Winterdiapause oder ihr Fehlen kennzeichnen die Überwinterungsstrategie dieser Arten.

7. Acknowledgements

I thank ARNE FJELLBERG and LAURITZ SØMME for commenting on a draft of this paper, JOHN G. ORMEROD for improving the English, and LISS FUSDAHL for typing the manuscript.

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Synopsis: *Original scientific paper*

LEINAAS, H. P., 1983. Winter strategies of surface dwelling Collembola. Pedobiologia **25**, 235—240.

Winter strategies of surface dwelling Collembola are described as sets of adaptations observed in winter animals. These adaptations play different roles in the life history of the species: Cold hardiness, anaerobiosis, and the ability to seek protected overwintering sites on the ground or up in the snow, are important factors for winter survival. Many species with patchy summer habitats have winter dispersal. Winter diapause or the lack of it mould the overwintering strategy of the species.

Key words: Collembola, insecta apterygota, overwintering strategies, surface dwelling species, adaptations, survival.